HABITAT ADAPTATIONS OF NORTH AMERICAN CAPRELLID AMPHIPODA (CRUSTACEA)

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Caprellid amphipods are common marine peracarid crustaceans that usually occur epibiotically and typically move on their substratum by crawling. Crawling consists of grasping the substratum with the gnathopods, releasing the grasp of the pereopods, and pulling the pereopods to a point just posterior of the gnathopods. At this point, the body is in an Omega-like configuration. The gnathopods are then released, the body is straightened, and the gnathopods again grasp the substratum. Caprellids do possess limited swimming capabilities, but powerful or directional swimming over a distance in excess of 15 cm has not been reported.

Specific substratum preferences are reported for a few caprellids, but the majority of species occur on a variety of organisms. The mechanism whereby a caprellid selects a substratum is unknown. As caprellids have direct development and, perhaps, limited powers of dispersal, Mayer (1882), McCain (1968), and Caine (in prep.) have indicated that rafting is the most frequent dispersal mechanism.

Some species with specific habitats have morphological adaptations to their substrata. Even those species occurring on different substrata may exhibit some substratum-specific morphological adaptations (McCain, 1968). Collections from Washington (Puget Sound, U.S.A.) yielded *Caprella gracilior* Mayer on the starfish *Luidia foliolata* Grube, *Mayerella banksia* Laubitz free on the bottom (not epibiotic), and *Perotripus brevis* (La Follette) on tubes of *Phyllochaetopterus prolifica* Potts. Each species exhibited morphological variations from "normal" caprellids.

This paper reports on the substratum-related morphological variations of North American caprellids, with emphasis on those appendages used in crawling.

MATERIALS AND METHODS

The caprellids are divided into four habitat categories: cosmopolitan substrata, starfish epibionts, gorgonian and bryozoan epibionts, and free on the bottom. Steriomicroscope observations on locomotion and stationary posturing were conducted on 15 species: *Caprella laeviuscula* Mayer (occurring in the northeastern Pacific, hereafter indicated by P), *C. natalensis* Mayer (P), *Caprella striata* Mayer (P), *Deutella californica* Mayer (P), *Luconacia incerta* Mayer (occurring in the northern Gulf of Mexico, hereafter indicated by GM), *Metacaprella kennerlyi* (Stimpson) (P), and *Tritella pilimana* Mayer (P)—cosmopolitan substrata; *Caprella greenleyi* McCain (P) and *C. gracilior* Mayer (P)—starfish epibionts;

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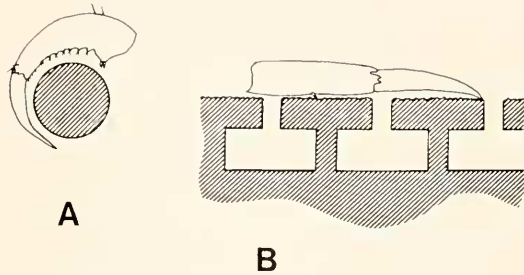
A

B

FIGURE 1. Grasping of the substratum by caprellid pereopods: A, encirclement (= typical mechanism); and B, grasping flat surface (= starfish epibionts).

Caprella penantis Leach (GM), *Paracaprella pusilla* Mayer (GM), and *P. tenuis* Mayer (GM)—bryozoan and gorgonian epibionts; and *Mayerella banksia* Laubitz (P) and *Perotripus brevis* (La Follette) (P)—free on the bottom.

Feeding mechanisms were observed following the methods of Caine (1977) with the specimens on their natural substrata. Stomach contents were examined in the segment of the digestive tract from the mouth to the end of pereonite III. More details are included for those species which only have been described taxonomically.

Species identifications were made with the aid of monographs by McCain (1968) and Laubitz (1970) and a paper by McCain (1969).

OBSERVATIONS AND RESULTS

Cosmopolitan substrata

All of the species occur on algae and hydroids, however, in my collections, *Caprella natalensis* occurs most frequently on Rhodophyta, *Deutella californica* on hydroids, and *Luconacia incerta* on attached *Sargassum*. All of the substrata are highly branched; the circumference of most branches of the substrata are small enough to allow encirclement by the pereopods so that the palmar portion of the propod contacts the substratum (Fig. 1A). Grasping spines, which occur proximally on the propodus (Fig. 2A), are in contact with the substratum.

An upright stance may occur when an animal is stationary. Grasping the substratum with the pereopods, pereonites VI and VII are in contact with the substratum. An angle of 90° is made at the articulation of pereonites V and VI; the remainder of the body is held vertically erect (Fig. 3A). Pereopod 5 of all of the cosmopolitan species examined herein is 6-segmented and usually inserted posteriorly on pereonite V.

Feeding mechanisms are dependent upon antennal and mouthpart setation; those species with swimming setae on the antennae are scrapers/filter-feeders, whereas those species without swimming setae obtain food by predation and scavenging (Caine, 1977).

Starfish epibionts

Caprella gracilior is a large caprellid occurring in dense populations on the aboral surface of *Luidia foliolata* Grube. *Luidia* is a large, subtidal starfish with
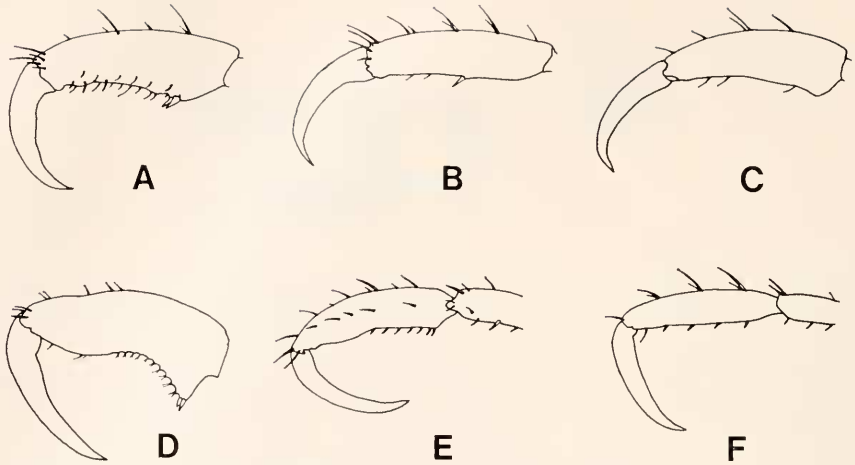
FIGURE 2. Structure and spination of the propod and dactyl of pereopod 7 as related to substratum type: A, cosmopolitan substrata (*Caprella laeviuscula*); B, starfish epibiont (*C. gracilior*); C, gorgonian epibiont (*C. penantis*); D, bryozoan epibiont (*Paracaprella pusilla*); and E and F, free on the bottom (*Mayerella banksia* and *Perotripus brevis,* respectively).

close-set paxillae and lacking prominent pedicellaria. The aboral surface is covered with small spines arising from the paxillae. Space between the paxillae varies slightly as the starfish moves its arms. General morphology of *C. gracilior* includes lack of prominent spination, sparse setation on the body and pereopods, the slender pereopods 5–7, and no true palmar development with a median grasping spine on the cylindrical propodi (Fig. 2B).

Crawling is typical (Fig. 1B) except that the substratum (starfish) is not encircled by the pereopods. Predominant feeding mechanisms are scraping and filter-feeding, but predation occurs frequently. Filter-feeding is similar to other caprellids (Wetzel, 1932; Caine, 1974, 1976, 1977); swimming setae on the antennae passively filter settling material from the surrounding water.

As observed, scraping is restricted to the capture of mucous secretions of the starfish and the settled material contained therein. Mucous capture occurs while the caprellid is stationary, but mucous strands are frequently located while the caprellid is crawling. Mucous strands are picked from the starfish with the first gnathopods, transferred to the maxillipeds and inner mouthparts, and ingested.

If a small organism (<3 mm) swims between the laterally spread gnathopods II and the anteriorly directed antennae while *C. gracilior* is in an upright stance, capture occurs as both pairs of antenna flex ventrally concurrent with medial movement of gnathopods II. During medial movement, the gnathopods are rotated so that the grasping margins contact the prey as the prey is forced into the grasp of gnathopods I. Epibenthic prey are captured as *C. gracilior* extends laterally from the arms of the starfish. The antenna do not assist in prey entrapment with this mode of predation, but the antennules did appear to guide prey into the grasp of gnathopod I by causing the potential prey to alter its direction of movement. When the prey moves near the cephalon, it is grasped by the first

gnathopods. Occasionally the mesioventral (broadside) portion of the propod of gnathopods II aid in prey capture by forcing the prey into the grasp of the first gnathopods.

This caprellid cleaned its antennae frequently. The dactyli of the maxillipeds and of the first gnathopods are crossed with the antennae that is being cleaned in the center. As the antenna is drawn anteriorly, material is transferred from the antenna to the maxillipeds. The material may be passed orally and ingested, or it may be concentrated on the dactyl of the maxillipeds and discarded. The fate of cleaned material is dependent on the amount of material on the antennae. The more material that is present, the greater is the chance that it will be discarded.

Caprella greenleyi was captured from intertidal algae and the aboral surface of *Henricia leviuscula* (Stimpson) inhabiting tidepools. *Henricia* is a small starfish that lacks a pedicellaria. *C. greenleyi* has small spines on pereonites V–VII, robust pereopods 5–7 with slight palm development, and each pereopod has a pair of grasping spines on the propod. Setation is short, but numerous, on the pereopods.

Feeding modes are restricted to scraping and filter feeding, with the major portion of the diet obtained by scraping. Crawling, antennal cleaning, and feeding are as described for *C. gracilior*.

Bryozoan and gorgonian epibionts

Adaptations to gorgonian hosts have been described by McCain (1968) for *Caprella penantis* and *C. equilibra*. He found a reduction in the ventral spine between gnathopods in *C. equilibra*. *C. penantis* has a reduction in pereopod setation and a reduction in the size and number of grasping spines (Fig. 2C). Caine (1974) examined feeding in *C. penantis* and observed the mucous secretions from the gorgonian host were used to increase particle entrapment by the antennae. However, most food materials are obtained by scraping the encrusting diatoms and detritus laden mucus from branches of the gorgonian.

Gorgonian branches are small enough to be partially encircled by the pereopod, and crawling is typical for the suborder.

Paracaprella pusilla and *P. tenuis* are most frequently captured among erect branching bryozoans (*e.g., Amathia* sp. and *Bugula neritina*). Both caprellid species have concave propodi on the pereopods which are proximally adorned with a pair of grasping spines and several knobs which increase in size proximally (Fig. 2D). The knobs have several short apical setae. Both species crawl in the typical manner, but when assuming an upright stance, *P. tenuis* frequently uses pereopod 5 to grasp a different substratum branch than that which is grasped by pereopods 6 and 7. Ambush predation (Caine, 1974, 1977) was the most frequently observed method of obtaining food for both species, but both commonly utilized alternate feeding modes.

Free on the bottom

Mayeralla banksia is a small caprellid existing free in dense populations on muddy sand substrata. Densities up to 38,750 m^{-2} were estimated from the largest sample (31 caprellids in an 8 cm^2 sample). *M. banksia* is seasonally abundant with populations most dense in the summer months, but ovigorous females have been
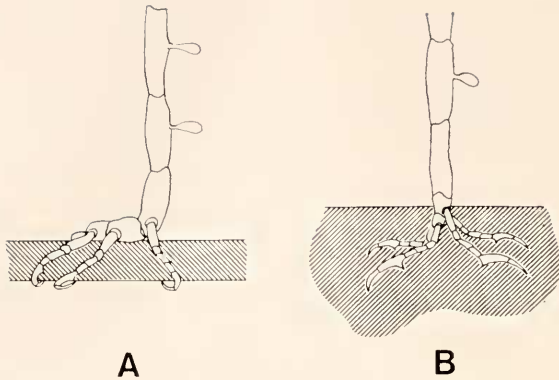
FIGURE 3. Upright stance of caprellids indicating the vertical height increase with the modified stance: A, typical stance with six-segmented pereopod 5; and B, modified stance with reduced pereopod 5.

captured in July and August. Morphological characters include the lack of swimming setae, overall body smoothness, pereopod 5 inserted near the midlength of pereonite V and reduced to three segments, and pereonite VII reduced. The propod of the pereopods has a weakly developed palm. Spines occur on the proximal half of the propod and spine density increases proximally; the dactyl is smooth, without spines or serrations (Fig. 2E). The anterior margin of the pereopods, the side facing the substratum when assuming an upright stance, is lined with spines from the merus to the propodus.

When stationary, *M. banksia* assumes an upright stance with the entire body held vertically erect (Fig. 3B). Support is achieved by placing the appendages on the surface of the substrata rather than by grasping; articulations of the short ischium allow an angle of 90° to be formed with the basis and the joints distal to the ischium-merus flexure remain outstretched. During crawling, the substrate is grasped by projecting the dactyl of the second gnathopods downward, into the substratum. Otherwise, crawling is similar to that of other caprellids except that the posterior portion of the body is anchored by the dactyls of pereopods 6 and 7 only.

Mayerella banksia readily releases its grasp of the substratum when physically disturbed and swims. Swimming movements are typical of caprellids (described by Jessen, 1969 and others), and the caprellid settles to the bottom after covering a distance of several cm (seldom more than 8–10 cm in still water).

Although the substratum appears to be highly organic (carbon examinations were not conducted), *M. banksia* relied on predation to obtain its nutrients rather than utilize the substratum directly. Prey organisms are mainly harpacticoid copepods, which are abundant in or on the substratum, but some small ostracods and gammarid amphipods are also captured. Scavenging occurs less frequently, but *M. banksia* does pick small objects from the substratum and ingests adhering material.

Mayerella banksia frequently cleans itself, especially the anterior appendages. Some of the material is ingested, but usually it is discarded. Antennal cleaning is similar to that of other caprellids with mandibular palps (Caine, 1976), *i.e.,* the

dactyli of the maxillipeds are uncrossed with the ventral area of the antenna contacted by the mandibular palps.

Perotripus brevis is a small caprellid occurring as epifauna on tubes of *Phyllochaetopterus prolifica* Potts in the very low intertidal (−0.9 m, below MLW). Only three collections of *P. brevis* were made, and these occurred in June and July. Ovigerous females and juveniles were found in the collections on all three occasions. This species lacks swimming setae, pereopod 5 is inserted near the midlength of pereonite V and is reduced to three segments, and pereonites II and III are pear-shaped. The pereopods are similar in structure to those of *Mayerella banksia,* except there is no palm development on the propod, spination occurs on the entire margin of the propod, and there is no proximal spine concentration on the propod (Fig. 2F).

The upright stance of *Perotripus brevis* is similar to that of *Mayerella banksia* (Fig. 3B), except that the sand grains cemented together to form the worm tubes are grasped by the appendages in the typical manner (Fig. 1A). The sand grains are grasped; encirclement of the worm tube does not occur. Swimming occurs only when repeatedly stimulated. The initial escape response is to crawl among the mass of worm tubes and then to remain still.

Perotripus brevis feeds primarily be predation. Harpacticoid copepods (0.20–0.31 mm) are the major prey. Prey are captured by rapidly bending the body and grasping the prey by the first gnathopods. The gut contents of *P. brevis* appeared to contain a lot of detritus and diatoms, but this material may have been the stomach contents of the harpacticoid prey. Abundant protozoans on the worm tubes may have also been ingested and rapid digestion of them would leave no trace in the stomach contents.

Observations were also made on intraspecific aggression of *Perotripus brevis.* Aggressive encounters resembled pushing matches where two opponents met, aligned their pereonites II and III, and pushed. The victor was the individual that pushed the opponent's pereonite V past vertical. The subordinate caprellid crawled away while the dominant remained stationary.

DISCUSSION

Podocerid amphipods, thought to be morphologically similar to the ancestral caprellid, include a group of species that occur epibiotically (Enequist, 1949; McCloskey, 1970). The pereopods (5–7) have numerous spines on the carpus or proximally on the propodus, and the palm is weakly developed (Laubitz, 1977). These forms have generalized grasping articles that, through centralization of the grasping spines, the inclusion of a palm, and increased prehensility (= rotation and subchelated) gave rise to the generalized caprellid pereopod structure (Fig. 2A). The primitive caprellids, *Caprogammarus* and *Cercops,* cosmopolitan species, and free living species all have generalized pereopods.

Starfish have grasping pedicellaria and may have paxillae. If paxillae are present, the space between the paxillae may vary as the starfish moves its arms. Either arm movement, *i.e.*, reducing the space between paxillae, or pedicellaria may entrap setae or spines. Relative to the size of the propod of the pereopod, the starfish provides a flat substratum which is contacted maximally by a cylindrical propod (Fig. 1B).

Those species regularly occurring on starfish substrata exhibit a loss of seta-
tion, a loss of grasping spines, and little palmar development (Fig. 2B). These
structures are secondarily derived as indicated by the advanced phylogenetic posi-
tion of most species reported as occurring on starfish: four species of *Caprella,
Aeginella spinosa,* and *Pariambus typicus. Caprella astericola, C. gracilior, C,
unica,* and *P. typicus* almost never occur on other substrata while *A. spinosa, C.
greenleyi,* and *C. linearis* only seldom are encountered on starfish. Thus, the
former group should be expected to exhibit greater substratum morphological
adaptations than the latter group. The pereopod of *C. greenleyi* is a form inter-
mediate between the cosmopolitan and starfish groups of caprellids.

The morphological results of an epibiotic existence of bryozoans and gorgonians
are similar, loss of spines and setae (Fig. 3C, D). However, the underlying
mechanism are different. Kaufmann (1971) has shown that the bird's head
avicularia of *Bugula* sieze the setae of amphipods crawling over the colony and that
the avicularia are structured so that maximum force is exerted on objects 0.05 mm
or less in diameter. Such a size range includes most setae on caprellids. While
these avicularia provide a mechanism to retard habituation by tube-dwelling gam-
marids, grasping is a tactile response (Kaufmann, 1971). Therefore, setae on
pereopods of caprellids would be grasped.

Gorgonians have no grasping structures, but imbeded in the coenchyme are
numerous tuburculate spicules. Coenchyme is soft and penetrated easily by both
setae and spines. As the gorgonian bends with the currents, the spicules of the
compressed side become closer together. Setae and spines may be trapped by
spicule movement. Similarly, the the ventral spine between gnathopods II on *C.
equilibra* would be abraded. From preliminary experiments and observations, it is
unclear if gorgonian-inhabiting caprellids initially possess spines and setae, which
are subsequently abraded, or if it is a genetic ecotypic variation.

Pereopods 6 and 7 are inserted posteriorly on their respective pereonites and
are six-segmented. Special attention is needed to explain insertion and size of
pereopod 5. Pereopod 5 is inserted from midlength to posterior on pereonite V.
Those pereopods that are inserted near the midlength may be six-segmented (as
with *Luconacia incerta*), diminished in size, or reduced (as with *Mayerella* and
Perotripus). Most genera with midlength pereopod 5 insertion have reduced
pereopods. As a result, species with reduced pereopods have a modified upright
stance (Fig. 2B).

All species of caprellids reported to exist free on the bottom have pereopod 5
inserted near the midlength and reduced. Contrasted with the epibiotic *Luconacia
incerta,* the conclusion may be drawn that reduction of pereopod 5 is a free-living
adaptation. As a result of pereopod 5 reduction, and concomitant upright
stance modification, the height of elevation from the bottom is increased without an
increase in body size. Visual predation may be maintained at a constant rate as
body size is constant. By modifying the upright stance, a wider search and capture
area for prey would result at the same body size. All caprellids that have reduced
pereopod 5 lack swimming setae, *i.e.,* they are predators and scavengers (Caine,
1977). However, a similar modified upright stance and increased capture areas
could be obtained by lengthening pereopod 5 rather than reducing it.

A second reduction mechanism may be that the site of pereopod 5 insertion is

not suitable for variability within a genus or subfamily, but that pereopod size is. If the caprellid with a normal pereopod 5 occurs epibiotically and assumes a typical upright stance, either pereonite V will be forced close to the substratum or pereopod 5 will not encircle the substratum. Selective forces would tend to reduce pereopod 5.

A third hypothesis is that grasping the substratum with four, rather than six, pereopods is an adaptation to quiet waters. *Maycrella* is most frequently reported from quiet waters with muddy bottoms. However, *Perotripus* is found in areas exposed to extensive surge action. Pereopod 5 is reduced in both species.

It is possible that all three hypotheses explain the reduction to some extent. This would account for the widespread correlation between midlength insertion and reduction of pereopod 5. Finding a free-living representative with posteriorly inserted pereopod 5 (not as with *Pariambus typicus* which occurs on the bottom after the starfish substratum buries itself) may cast doubt on the validity of the search/capture hypothesis, but such doubt should not be formed from an epibiotic representative with reduced pereopod 5.

Further generalizations can be made regarding substratum-feeding relationships. Feeding in the Caprellidea has been seldom studied, and feeding mechanisms of relatively few species are known. However, Caine (1977) correlated the feeding of species that have been studied with the presence or absence of swimming setae. Those species with swimming setae obtain a majority of their food items by scraping or filter-feeding, while those species without swimming setae primarily rely on predation or scavenging, although scraping occurs regularly.

Caprellids usually occur in those habitats that maximize their feeding effectiveness. Within most filamentous substrata (hydroids, bryozoans, algae, etc.), no feeding mode is favored. However, gorgonians and starfish support relatively few prey species and, if observations on feeding are correct, those species with swimming setae should be more frequently encountered. *Pariambus typicus*, on the starfish *Asterias* and *Crossaster*, is a notable exception, and it is probable that *P. typicus* obtains most of its food materials by capturing mucous strands from the starfish.

Those species living free on the bottom, in contrast, are without swimming setae. Living on or within the surface layers are numerous harpacticoid copepods, ostracods, nematodes, and some gammarid amphipods upon which to prey. Flocculent material is usually silty, not detritus, and few suitable objects for scraping occur. Therefore, species existing free on the bottom should not have swimming setae.

SUMMARY

1. Caprellid amphipods occur epibiotically or free on the bottom. There are four general types of substrata and caprellids have distinctive morphological adaptations to each substratum type.

2. Those caprellids without specific substratum preferences have primative propod structure including proximal grasping spines and distinct palm development.

3. Starfish epibionts have cylindrical propods and both setae and spines are reduced. Bryozoan and gorgonian epibionts have morphological adaptations similar to starfish epibionts, but the selective forces for the parallelism differ between the two groups.

4. Caprellids existing free on the bottom have reduced pereopods 5, which result in a modified upright stance. The modified upright stance allows a greater prey search area without an increase in body size.

5. Various substratum types support different arrays of available food for the caprellids. Gorgonians and starfish generally support scraping/filter-feeding species while those species regularly occurring free on the bottom are predators. No feeding type is favored on most filamentous substrata.

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